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Speed Discrimination of Distal Stimuli during Smooth Pursuit Eye Motion

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We evaluated the hypothesis that smooth pursuit eye movements affect speed discrimination thresholds of distal stimuli because they alter the retinal image speed. Subjects judged speed differences of sine-wave gratings while they simultaneously pursued a superimposed moving bar. Speed discrimination thresholds were measured, under conditions of controlled eye movements, for grating speeds of 0.5 and 2.0 deg/sec across a range of eye velocities. Thresholds were simulated using a Monte Carlo method based on the retinal speed hypothesis, and the simulation predictions were compared to the psychophysically determined thresholds. The simulation results provided a good match to the psychophysical data for conditions where the eye moved at a slower speed than the grating, regardless of whether the eye moved in the same or opposite direction. However, when the eye moved at a faster speed than the grating in the same direction, the psychophysical thresholds were significantly higher than predicted by the simulation. Control experiments and analyses rule out explanations based on relative motion cues, saccadic involvement, and attentional demands. Copyright © 1996 Elsevier Science Ltd.

Speed discrimination Eye movements Retinal image motion Smooth pursuit eye movements

INTRODUCTION

We frequently make judgments about speed differences of objects in the world. When we make these judgments our eyes are moving, unless we purposely maintain fixation on a stationary target (Kowler & McKee, 1987). The smooth pursuit eye movements sum with the distal stimulus motion in a vectorial manner to produce the retinal motion. Thus, a direct consequence of eye movements is a transformation of the retinal image motion of the distal stimulus.

Consider the retinal motion effects of variously moving objects within a scene, as a person makes smooth pursuit eye movements (Fig. 1). Case 1: when the eye moves in the opposite direction to an object within a scene, the retinal motion of that object will be faster than when the eye is stationary. Case 2: when the eye moves in the same direction as the object but at a slower speed, the retinal motion will be slower than when the eye is stationary. Case 3: when the eye moves in the same direction as the object but at a faster speed, the direction of the retinal image motion will be opposite to the eye motion as well as opposite to the retinal image motion that is produced when the eye is stationary.

Thus, the speed and direction of the retinal image motion can be altered by eye movements. This fact, taken together with the understanding that the retinal image motion is processed by the visual system and used to derive decisions about the distal stimulus, suggests that eye movements may affect the precision of speed judgments about distal stimuli.

In experimental situations where eye movements are minimized, either by having subjects maintain fixation on a stationary mark (McKee, 1981; Orban *et al.*, 1984; Pantle, 1978) or with image stabilization (Heidenreich & Turano, 1996; Turano & Heidenreich, 1993), retinal speed closely matches the distal stimulus speed. Under these conditions, speed discrimination thresholds for reference speeds up to 16 deg/sec asymptoted at approximately 5–10% of the reference speed.

Previously, we (Heidenreich & Turano, 1996; Turano & Heidenreich, 1993) explored whether speed discrimination improves when the retinal image is stabilized against the effects of eye movements. The results showed that speed discrimination thresholds were comparable for unstabilized and stabilized conditions for reference speeds greater than approximately 1 deg/sec. For example, thresholds for a 2 deg/sec reference speed were 0.23 deg/sec in stabilized viewing and 0.22 deg/sec in unstabilized viewing. However, for slower reference speeds, discrimination thresholds were higher for stabilized conditions relative to unstabilized conditions. For a

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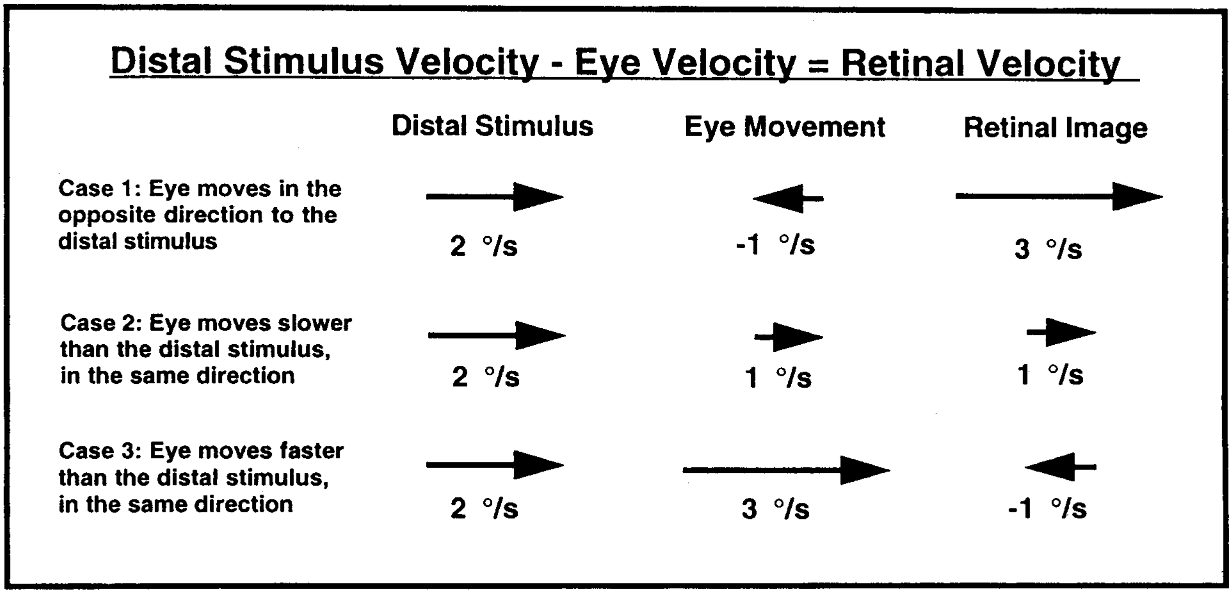


FIGURE 1. Illustration of eye movement effects on retinal velocity for a fixed distal stimulus velocity.

0.5 deg/sec reference speed, thresholds were 0.17 deg/sec in stabilized viewing and 0.10 deg/sec in unstabilized viewing. We recorded eye movements during the unstabilized conditions, to obtain an estimate of the retinal image speed. We showed that speed discrimination thresholds obtained with image stabilization were similar to those obtained in unstabilized conditions when the unstabilized thresholds were expressed as a function of the estimated *retinal speed*. In other words, eye movements affected speed discrimination thresholds only insofar as they altered the speed of the retinal image.

In this study we directly evaluated the hypothesis that smooth pursuit eye movements affect speed discrimination thresholds in a manner consistent with the transformed retinal speed. Speed discrimination thresholds were simulated using a Monte Carlo method based on the retinal motion hypothesis. Speed discrimination thresholds were measured under conditions of controlled eye movements, and the results were compared to the simulation predictions. The results showed that the retinal motion hypothesis can account for subjects' speed discrimination performance in conditions where the eye moves in the opposite direction to the distal stimulus (Case 1) and in conditions where the eye moves in the same direction as the distal stimulus but at a slower speed (Case 2). The model cannot account for performance in conditions where the eye moves in the same direction as the distal stimulus but at a faster speed (Case 3).

METHODS

Computer simulation methods

Procedure. Speed discrimination thresholds were simulated for grating speeds of 0.5 and 2.0 deg/sec across a range of eye velocities. The probability density functions that were used in the simulation were derived from the speed discrimination functions obtained previously with image stabilization (Heidenreich & Turano, 1996; Turano & Heidenreich, 1993).* Figure 2 shows the parameters, α and β, of the best fit Weibull functions [equation (1)] to the speed discrimination data obtained under image stabilization for speeds ranging from 0.5 to 4 deg/sec. The parameter α specifies the threshold (delta speed where performance is 82% correct) and the parameter β specifies the slope of the psychometric function

$$f(x) = 1 - 0.5 * \exp[-(x/\alpha)^{\beta}]. \quad (1)$$

These relations are well described by second-order polynomial functions, shown as the solid and dashed lines (subjects KT and SH, respectively). For subject KT

$$\alpha = 0.1767 + 0.0455 * s + 0.0176 * s^2 \quad (2)$$

$$\beta = 0.5683 + 0.9699 * s - 0.1864 * s^2 \quad (3)$$

where s is retinal speed in deg/sec. For subject SH

$$\alpha = 0.2310 - 0.0450 * s + 0.0424 * s^2 \quad (4)$$

$$\beta = 1.1090 + 0.7956 * s - 0.2249 * s^2. \quad (5)$$

From these datasets, we were able to generate proportion-correct distributions for *retinal speed differences*, given any specified retinal reference speed.

Each simulation was run with a single reference speed and a single mean eye velocity. On each trial, in one of two intervals the grating moved at the reference speed and in the other interval it moved at a test speed (reference speed plus a delta speed). Delta speed was initially set at 0.05 deg/sec and was subsequently incremented by 0.05 deg/sec. Each delta speed was run

*These data are similar to the data obtained in studies where a stationary fixation point served to minimize eye movements (McKee, 1981; Orban *et al.*, 1984; Pantle, 1978). The selected datasets have the advantage that the thresholds measured with image stabilization were obtained from the same two subjects who served in the present study.

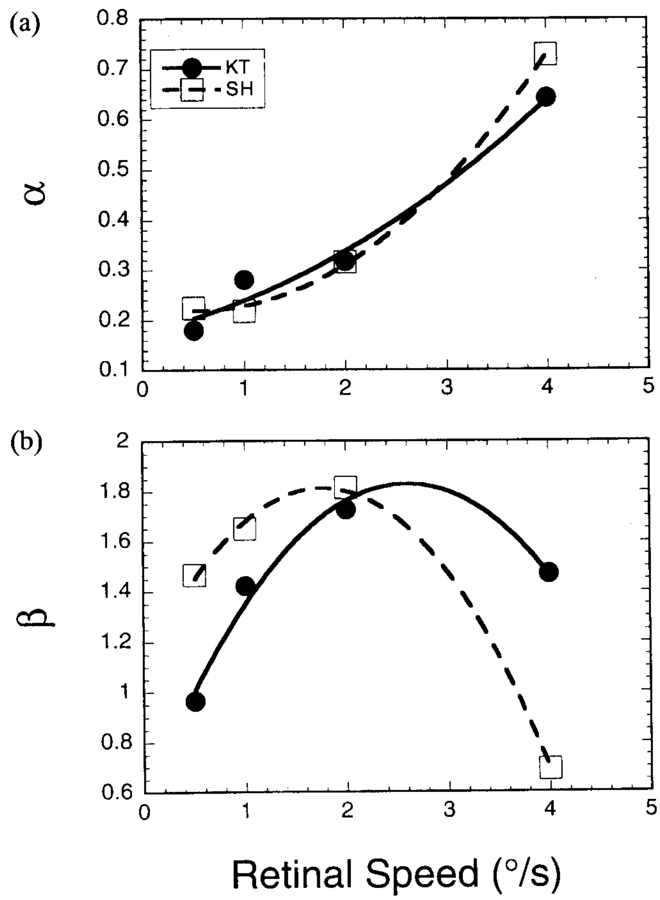


FIGURE 2. The Weibull parameters, α (a) and β (b) plotted against estimated retinal speed. The parameters are from the best fit Weibull functions to the speed discrimination data obtained under image stabilization (Heidenreich & Turano, 1996; Turano & Heidenreich, 1993). Solid symbols: subject KT; open symbols: subject SH. Curves are the best second-order polynomial fits.

100 times. For each of the two intervals, eye velocity was randomly selected from a gaussian distribution (mean eye velocity, standard deviation 10% of the mean*). Retinal velocities were calculated for the two intervals and the difference between the two retinal velocities, the retinal speed difference, was computed. The computer's task was to choose the interval of the faster moving grating. Computer responses were guided by the aforementioned probability-correct distributions for each trial's calculated retinal reference speed. The computer either correctly or incorrectly chose the faster of the two intervals based on the probability of correct response for the particular retinal speed difference. To determine thresholds for the simulation, Weibull functions [equation (1)] were fit to the distributions of simulated proportion-correct responses.

*Trial-to-trial variability (standard deviation) of eye speed has been shown to range from 3 to 30% of the mean eye speed (Kowler & McKee, 1987; Kowler *et al.*, 1978; Murphy, 1978). For the present simulation, we used an intermediate value (10%) to estimate trial-to-trial variability.

Psychophysical methods

Subjects. Two experienced psychophysical subjects (the authors, K.T. and S.H.) participated in the experiment. Both subjects had normal or corrected-to-normal vision, with visual acuities of 20/17.

Stimuli. The stimuli were generated by a graphics display board (Cambridge Research Systems), controlled by an IBM-compatible AT computer, and displayed on a Joyce DM2 monitor with a refresh rate of 100 Hz. The display was 5.6 deg high by 8.6 deg wide. (Thresholds measured with a circular display, 5.6 deg diameter, did not vary from those measured with the rectangular display in an appreciable manner.) Viewing distance was at 2 m, except when otherwise noted. The distal stimulus was a vertically oriented, 3 c/deg sine-wave grating, at 20% contrast. The reference speed of the grating was 0.5 or 2.0 deg/sec depending on the experimental condition. A vertical bar (0.06 deg wide by 5.6 deg high, 10% positive contrast) served as the pursuit stimulus that moved across the display screen at a specified velocity. The bar and grating velocities were independent of each other. Throughout each experimental session, the pursuit bar moved across the display screen at a constant velocity and wrapped around when it reached the edge. The observer was instructed to keep her eye on the bar during each experimental trial.

Design and procedure. Psychophysical speed discrimination thresholds were determined by a two-alternative, forced-choice procedure. A tone indicated the start of each trial. On each trial, in two successive intervals, a drifting grating was presented with a superimposed pursuit bar (Fig. 3). The duration of each interval was 450–550 msec, randomly determined. The time between intervals was 1 sec. In one of the randomly selected intervals, the grating moved at the reference speed, and in the other interval, the grating moved at the test speed which was the reference speed plus a delta speed. The subject's task was to indicate which interval contained the faster moving grating. Auditory feedback was given. The time between trials was approximately 3.5 sec. The two gratings always moved in the same direction, right or left, and, due to system limitations, the direction of motion remained fixed throughout the experimental session. Direction of grating motion was systematically alternated across test sessions. The potential for direction-specific adaptation was the same across conditions. Furthermore, the similarity between the results obtained in the "fixed direction" conditions and those obtained in the second control experiment, where the direction of motion was randomized between trials, indicates that the fixed direction of grating motion did not affect the results.

Delta speed varied from trial to trial according to a staircase procedure. Delta speed, initially set at 50% of the reference speed, was always added to the reference speed to produce the test speed. This was done to maintain procedural compatibility with the image stabilization study (Heidenreich & Turano, 1996; Turano & Heidenreich, 1993). After two consecutively correct

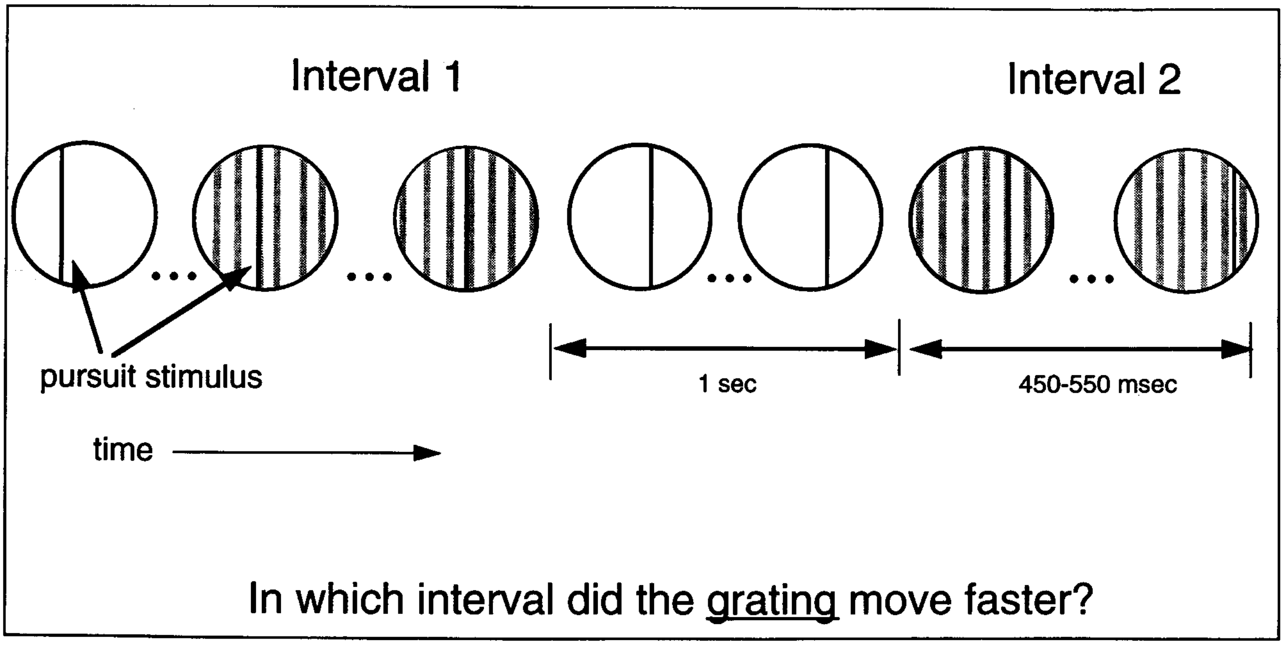


FIGURE 3. Illustration of the time course in an experimental trial.

judgments, the delta was decreased by half. After a single incorrect response, the delta was increased in a similar manner. Data collection began after the third reversal or if the delta reached 0.05. The test session ended after 16 reversals were made. Speed discrimination thresholds were obtained by fitting a Weibull function [equation (1)] to the distribution of proportion-correct responses for delta speed.

Eye movement recording. Since the speed of smooth pursuit eye movements does not always match the speed of the pursuit stimulus (cf., Kowler, 1990), we measured actual eye velocity throughout the experiment using an SRI Generation-V dual Purkinje-image eyetracker (Crane & Steele, 1985). Eye velocity was determined from the voltage analogs of horizontal eye position. The voltages were fed into an analog-to-digital converter every 10 msec and stored on a computer for off-line analysis. Voltage was converted to degree of visual angle, based on each subject's calibration results. The calibration procedure was as follows: twenty-five equally spaced points, extending 6 deg horizontally and vertically, were displayed in sequence on a CRT display screen positioned 2 m in front of the subject. To calibrate each point, a central dot appeared and the subject pushed a button when she fixated the point. Then the central dot disappeared, a calibration dot appeared, and the subject fixated the point. At that time, the voltage and the screen position of the dot were recorded. To convert voltage to degrees of visual angle, a regression line was fit to the dots' horizontal positions, expressed in terms of visual angle, plotted against the horizontal positions of the eye, expressed in terms of voltage.

Eye velocity was computed as the slope of the best-fit regression line of horizontal eye position over time. Prior to calculating pursuit eye velocity, saccadic eye movements were identified and eliminated in a manner similar to Dursteler and Wurtz (1988). Specifically, prior to analyzing the eye records, a threshold velocity was set (14 deg/sec) and any two successive data points whose calculated eye velocity exceeded the threshold were eliminated from the eye record along with the next four data points. For motion sequences in which data points were removed, eye velocity was defined as the weighted average of the separately computed slopes for the individual segments.

Average eye velocity for each condition was defined as the mean of the eye velocities measured in the reference speed intervals of each trial. In Fig. 4 average eye speed (magnitude of the velocity vector) is plotted against pursuit bar speed. The circles and squares represent eye speeds measured with the 2.0 and 0.5 deg/sec gratings, respectively. Pursuit data with a gain of 1.0 (gain = eye speed/pursuit stimulus speed) would fall on the dashed diagonal line. The magnitude of the deviation from the dashed line indicates the mismatch between bar and eye speeds.

The mean of the gains for the 2.0 deg/sec grating conditions with bar and grating moving in the same direction are 0.81 (SD = 0.17) and 0.98 (SD = 0.33) for subjects KT and SH, respectively. When the bar and grating moved in opposite directions the mean gain dropped by 6% to 0.76 (SD = 0.10) for subject KT (subject SH did not participate in the opposite direction conditions).

For the 0.5 deg/sec conditions with bar and grating moving in the same direction the mean gains are 0.86 (SD = 0.51) and 1.36 (SD = 0.80) for subjects KT and SH, respectively. When the bar and grating moved in opposite directions the mean gain remained nearly the same, 0.86 (SD = 0.25) for subject KT.

The lack of unity gain underlines the importance of measuring eye velocity in experiments where eye

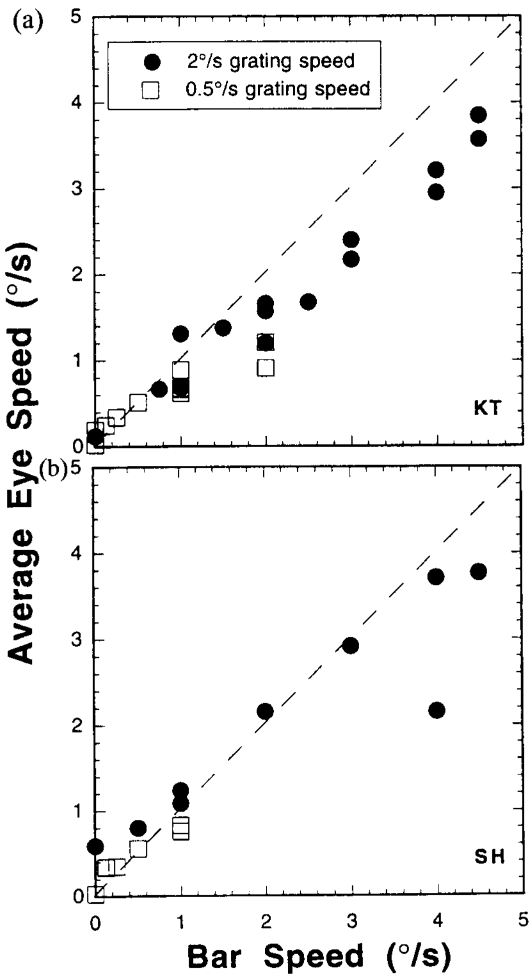


FIGURE 4. Average eye speed plotted against pursuit bar speed. Circles: 2 deg/sec gratings; squares: 0.5 deg/sec gratings. (a) subject KT; (b) subject SH.

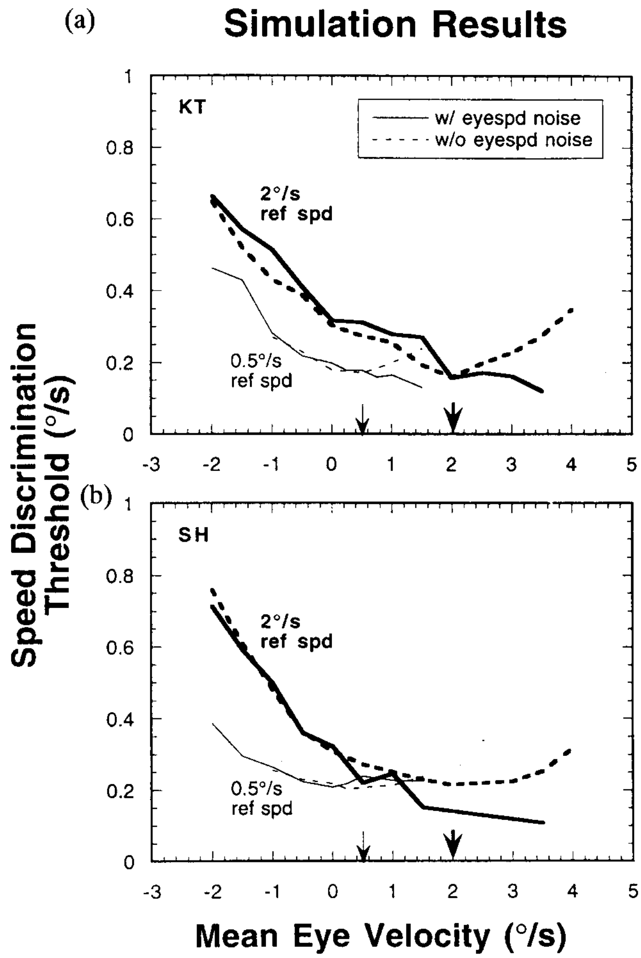


FIGURE 5. Simulated discrimination thresholds plotted against mean eye velocity. Thick lines: 2.0 deg/sec grating; thin lines: 0.5 deg/sec grating. Solid lines: simulation with variability in eye velocity; dashed lines: simulation without variability in eye velocity. Negative values of eye velocity indicate eye motion in the opposite direction to the grating and positive values indicate eye motion in the same direction. (a) subject KT; (b) subject SH.

velocity is discussed. One must be cautious when interpreting the results of experiments in which eye velocity is merely assumed to equal pursuit target velocity.

Previous investigators have shown a slight reduction in the mean gain when subjects track a target moving across a stationary, textured background (Collewijn & Tamminga, 1984; Kowler *et al.*, 1984) as well as when subjects track a transparent pattern (Niemann *et al.*, 1994). Our finding of a 6% gain reduction in the 2.0 deg/sec condition for opposite directions is comparable to the small amount of gain reduction reported in past studies, i.e., 0.5–10%.

RESULTS

Simulation results

The simulation predictions generated from the Monte Carlo method are shown in Fig. 5 as a function of mean eye velocity. Negative values of eye velocity indicate eye motion in the opposite direction to the grating, and positive values indicate eye motion in the same direction. The top graph shows simulation results derived from subject KT's image stabilization data [equations (2) and (3)] and the bottom graph shows results derived from subject SH's data [equations (4) and (5)]. The thick and thin lines represent simulation results for the 2.0 and 0.5 deg/sec gratings, respectively. As a visual aid, thick and thin arrows are positioned at the corresponding grating speeds. The solid curves represent results of simulations where eye velocity was randomly selected from a gaussian distribution with a standard deviation set at 10% of the mean. For the purpose of comparison, simulations were also run where eye velocity was fixed at the mean eye speed (i.e. standard deviation = 0), and the results are shown as the dashed curves.

As shown in Fig. 5, the retinal motion hypothesis predicts that eye movements will affect speed discrimination thresholds. If we look at the simulation predictions generated without eye velocity variability (the dashed lines in Fig. 5) we find that as the eye speed deviates from the grating speed, thresholds increase. The main difference in the predictions generated with eye velocity

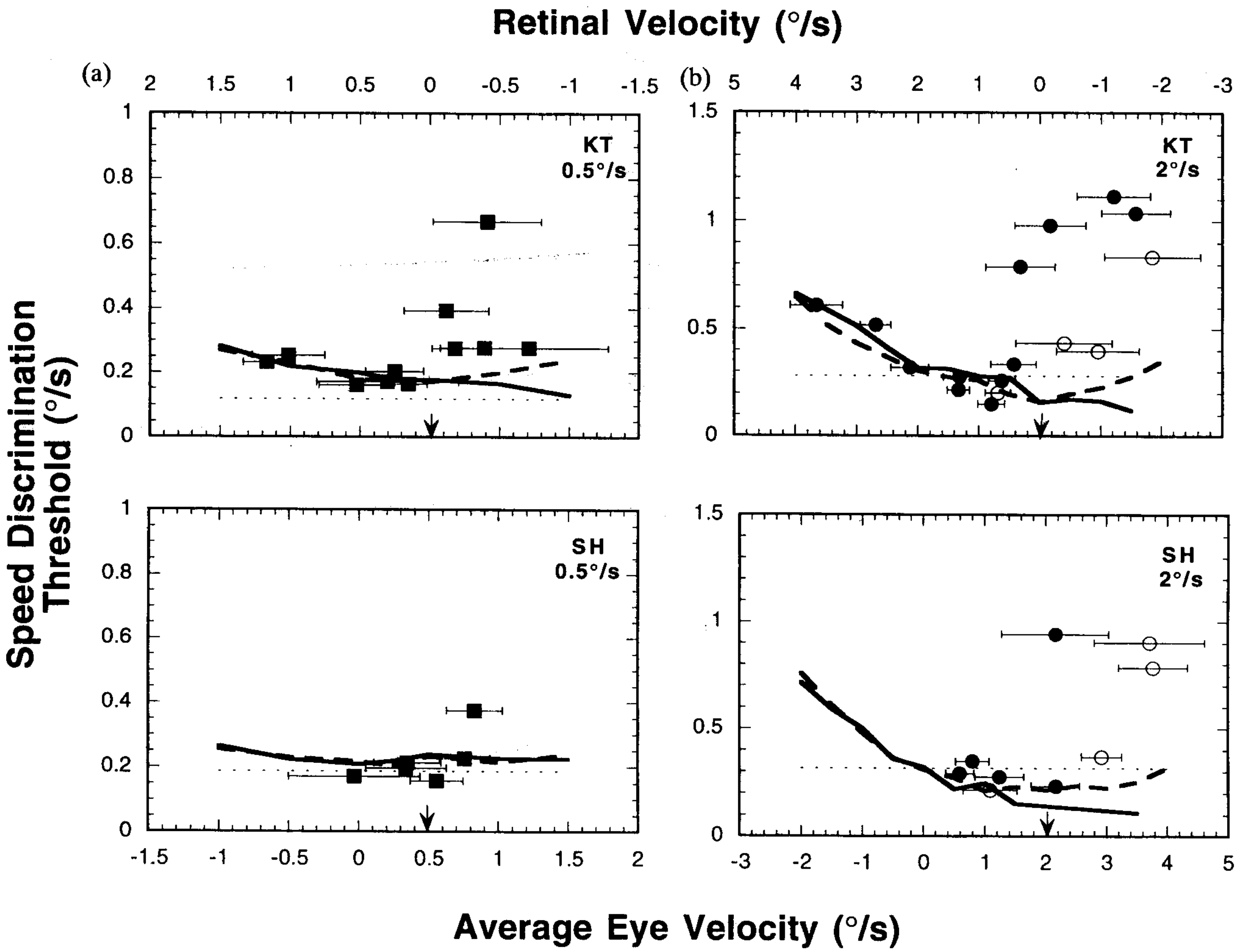


FIGURE 6. Speed discrimination thresholds plotted as a function of average eye velocity (lower x-axis) and retinal velocity (upper x-axis). Negative velocity values indicate motion in the opposite direction to the grating. Solid lines: simulation with variability in eye velocity; dashed lines: simulation without variability in eye velocity. Dotted lines: threshold in the absence of a pursuit stimulus. Solid symbols: 2 m viewing distance; open symbols: 1 m viewing distance. (a) 0.5 deg/sec grating; (b) 2 deg/sec grating. Reference speeds denoted by arrows. Top: subject KT; bottom: subject. SH.

variability is that for eye movements faster than the grating, in the same direction, thresholds do not systematically increase with eye speed. Although the latter is the more likely scenario given the reported estimates of variability in past pursuit studies (Kowler & McKee, 1987) we have included the results of the other simulation to demonstrate the magnitude of the effects that can be attributed to the variability of eye velocity.

Psychophysical results

In Fig. 6, speed discrimination thresholds are plotted as a function of the average eye velocities. (Retinal velocity is denoted on the upper x axis.) (a) and (b) represent the psychophysical data combined with the simulation results for the 0.5 and 2.0 deg/sec gratings, respectively. Psychophysical data are shown as symbols, and the simulation results are shown as thick lines (solid lines represent results obtained with variable eye velocity and dashed lines represent results obtained with fixed eye velocities). The dotted lines indicate the threshold levels obtained when no pursuit stimulus was present.

In our study, both the psychophysical and simulation threshold values are at 82% correct performance. This corresponds to a d′ value of 1.29 for a two-alternative, forced choice, a value higher than commonly used in many previous speed discrimination experiments (McKee, 1981; Orban *et al.*, 1984; Pantle, 1978). To roughly compare threshold values of the present study to threshold values reported by McKee (1981), for example, who used a threshold of 62.5% correct (d′ $\sim$ 0.45), the present threshold values must be divided by 2.9. Thresholds for eye velocities near 0, i.e., 0.3 deg/sec for the 2.0 deg/sec gratings and 0.17 deg/sec for the 0.5 deg/sec gratings, when transformed are approximately the same as those reported in other speed discrimination studies.

If eye movements have no effect on speed discrimination performance, then the data should fall on a horizontal line whose y-intercept equals the threshold for a 0 deg/sec eye velocity. If eye movements have an effect on speed discrimination performance and the effect is totally explainable in terms of retinal image motion, then the data should fall near the model predictions, with about as much variability as is shown by the simulation results. As shown in Fig. 6, the data do not totally comply with either of these two predictions.

As shown in Fig. 6, when the eye moves in the opposite direction to the grating (Case 1), thresholds increase with increasing eye velocity. Psychophysical data in this range closely match the simulation predictions (average mean square error of 0.003), supporting the retinal motion hypothesis. When the eye moves in the same direction as the grating, and at a slower speed (Case 2), thresholds either remain fairly constant (0.5 deg/sec conditions) or they decrease slightly (2.0 deg/sec conditions). The psychophysical data in this range also match the simulation predictions reasonably well (average mean square error of 0.002). However, when the eye moves faster than the grating, in the same direction (Case 3), thresholds are significantly elevated. In this range, there is a large discrepancy between the psychophysical data and the simulation predictions (average mean square error of 0.086).

For the 2.0 deg/sec gratings, the eye velocities tested in Case 3 were faster than 2 deg/sec. With a display size limited to 5.6×8.6 deg, fast pursuit speeds increased the likelihood of saccades within a trial. With the faster speeds, the eye reached the edge of the display and executed a retrace saccade more frequently than with the slower speeds. In fact, the eye records showed saccadic eye movements on more than 90% of the trials. Although saccadic eye movements were eliminated prior to the calculation of average eye velocity, the presence of a large number of them within an experimental condition may have contributed to the subjects' poor performance. In order to measure thresholds at eye velocities faster than 2 deg/sec, without the intrusion of saccades, we re-measured a subset of the thresholds using a larger display size, accomplished by reducing the viewing distance to 1 m. At the shorter viewing distance the display size doubled. The eye records showed that fewer than 4% of the trials contained saccades. Data obtained at the closer viewing distance are plotted in Fig. 6 as open symbols. The results show that even in the absence of saccadic eye movements, thresholds are elevated for conditions where the eye moves at a faster speed than the grating, in the same direction.

Control experiment: Relative motion between bar and grating. In our study, the drifting grating and bar were superimposed, creating a potential relative motion cue. We ran a control experiment to exclude the possibility that performance was governed by the strength of the relative motion cues alone. Specifically, we measured speed discrimination thresholds for a 0.5 deg/sec grating across a range of bar speeds, as subject KT fixated a stationary target. With this procedure, the eye remained relatively still (i.e., average eye velocity was less than 0.1 deg/sec) as the speed of the relative motion varied. If the variation in speed discrimination thresholds with eye velocity was not a direct consequence of a moving eye, but rather the effect of relative motion between the bar and grating,* then eliminating (or minimizing) eye movements during the experiment should not change the results.

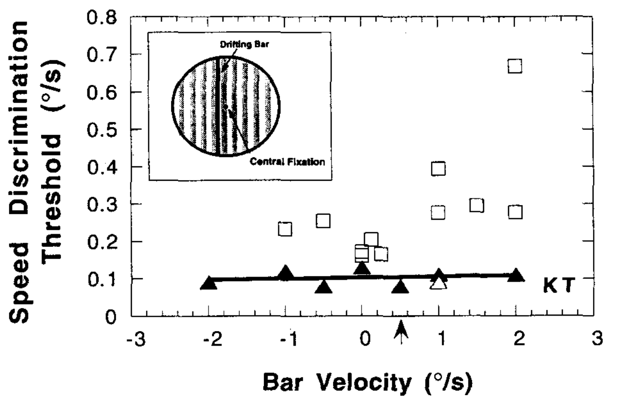


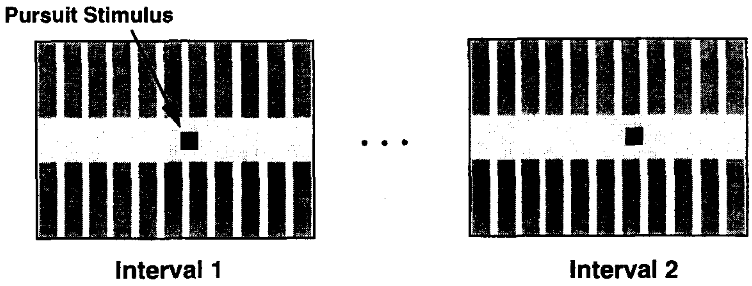
FIGURE 7. Speed difference thresholds plotted against bar velocity. Solid symbols: centrally located, stationary fixation mark; open triangle: peripherally located, stationary fixation mark; open squares: pursuit data replotted from Fig. 6(a). Line is the best linear fit to the data obtained with a centrally located, stationary fixation mark. Grating speed = 0.5 deg/sec, subject KT.

Figure 7 shows speed discrimination thresholds as a function of bar velocity. Data obtained with a stationary fixation point are plotted as closed triangles, and data obtained during pursuit (Fig. 6) are replotted as open squares. The open triangle represents the threshold for a peripherally located (edge of display screen) stationary fixation point. The results show that, despite the presence of the relative motion between the drifting bar and grating, thresholds vary only slightly across a range of bar speeds when the eye is stationary. The difference in the pattern of results obtained with a moving and a stationary eye indicates that the elevated thresholds during the pursuit experiment are not simply due to the presence of relative motion between the bar and grating.

Control experiment: Superposition of bar on grating. We ran a second control experiment to determine whether the elevated thresholds of Case 3, where the eye moves at a faster speed than the grating in the same direction, persist when the pursuit stimulus is spatially separate from the grating. In this experiment, the subject pursued a small square that was positioned within a horizontal strip of uniform luminance located across the midsection of the display (illustrated in Fig. 8).

Stimulus generation and data collection were controlled by a Macintosh IIci, equipped with a video board that permitted two monitors, one for stimulus generation and the other for parameter specifications. The stimuli were presented on an Apple high resolution RGB monitor with a 66.7 Hz raster rate. Prior to testing, the monitor was calibrated to linearize a range of voltage–luminance

*Under conditions of minimal eye movements, the relative retinal motion of the bar and the grating is comparable to the relative distal motion.



Grating speed (°/s)	1.0	1.0
Eye speed (°/s)	0.7	2.5
Δ thr (°/s)	0.14	0.60
Simulation w/ eyespd variability	0.23	0.22
w/o variability	0.22	0.25

FIGURE 8. Illustration of display configuration for the superposition control experiment along with a table of the speed discrimination thresholds.

values and to permit computation of a gamma correction for each gun. The display was 3 × 10 deg at the viewing distance of 1.35 m. The stimulus, a vertically oriented, 3 c/deg sine-wave grating was divided in half by a horizontal strip (0.5 deg in height) that extended the entire width of the screen. A small square (0.25 deg) that served as a pursuit stimulus was centered within the horizontal strip. The mean luminance level was 25 cd/m^2, with a contrast of 30%. The luminance level of the horizontal strip was equal to the mean luminance of the grating stimulus. The grating reference speed was 1.0 deg/sec and thresholds were measured for two eye velocities, 0.7 deg/sec (square speed = 0.5 deg/sec) and 2.5 deg/sec (square speed = 4.0 deg/sec). The bar moved in the same direction as the gratings. The two gratings always moved in the same direction, right or left, and the direction of motion was randomly determined trial to trial. The procedure was the same as employed in the original experiment, i.e., two-alternative, temporal forced-choice procedure. After the two gratings were successively presented, the subject judged which of the two was faster, by depressing one of two keys on a keyboard.

Figure 8 shows a table of the psychophysical results and the simulation predictions. The speed discrimination threshold measured when the eye moved slower than the grating was 0.14 deg/sec. When the eye moved faster than the grating, the threshold increased significantly to 0.60 deg/sec, a value almost three times higher than the 0.22 deg/sec Monte Carlo simulation prediction. The pattern of results in this control condition is similar to that obtained in the original experiment where the pursuit bar and grating were superimposed; thresholds are elevated relative to the retinal motion prediction when the eye moves faster than the grating, in the same direction.

DISCUSSION

The present study demonstrates that pursuit eye movements can affect an observer's ability to detect small differences in the speed of distal stimuli. The critical factor does not appear to be eye speed, *per se*, but rather eye velocity relative to the distal stimulus velocity. To illustrate, speed discrimination for a 2.0 deg/sec distal stimulus is little affected by a 1 deg/sec eye movement in the same direction (Fig. 6). However, the same eye velocity results in a threshold doubling when the distal stimulus moves at 0.5 deg/sec.

The results of a Monte Carlo simulation indicate that the speed discrimination thresholds can, in certain cases, be attributed to the transformation of retinal image speed that occurs with eye movements. Speed discrimination performance depends upon the speed of the retinal image, and eye movements alter the retinal image speed. Thus, it is reasonable to expect that speed discrimination performance will be affected by eye movements. In Case 1, where the eye moves in the opposite direction to the distal stimulus, and in Case 2, where the eye moves in the same direction as the distal stimulus but at a slower speed, the predictions generated by a Monte Carlo simulation based on the retinal motion hypothesis closely match the psychophysical data. In Cases 1 and 2, distal stimulus motion and eye motion have equal effects on speed discrimination performance. This is reminiscent of Murphy's (1978) finding that externally imposed and self-imposed retinal image motions have equal effects on contrast detection.

However, transformed retinal speed cannot account for the elevated thresholds measured when the eye moves faster than the distal stimulus, in the same direction. Some other factor is needed to account for the Case 3 results.

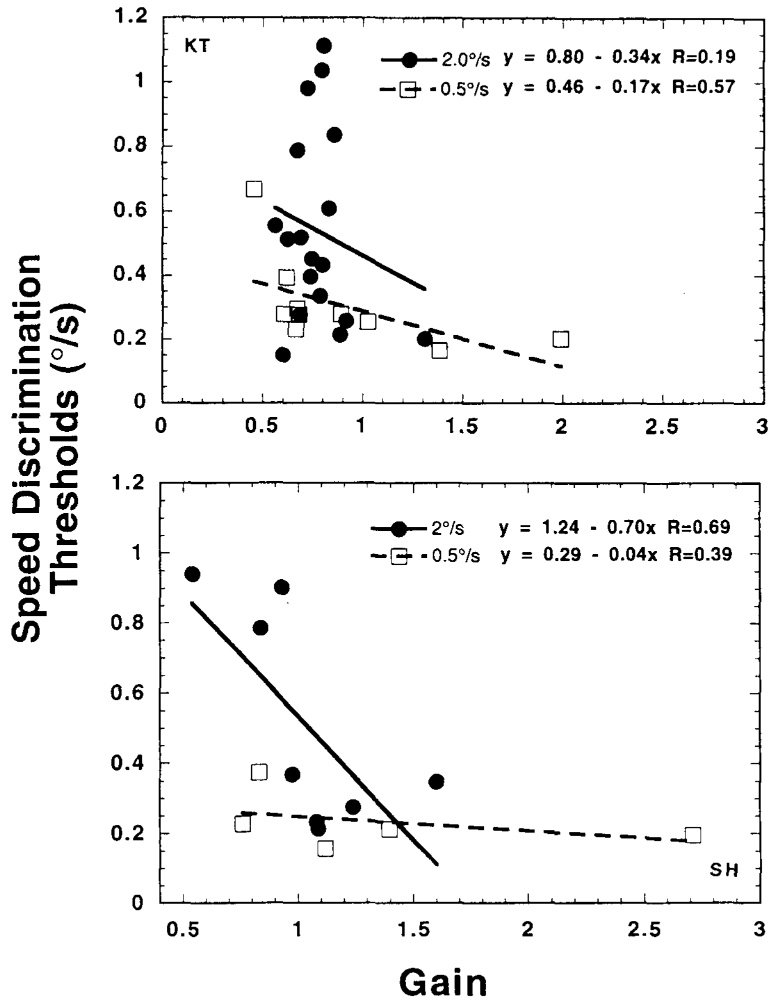


FIGURE 9. Speed difference thresholds plotted against gain (eye velocity/pursuit stimulus velocity). Solid symbols: 2 deg/sec grating; open symbols: 0.5 deg/sec grating. Lines are the best linear fits. Top: subject KT; bottom: subject SH.

Interference between concurrent visual tasks

Kowler and colleagues (Khurana & Kowler, 1987; Kowler *et al.*, 1984) have shown that oculomotor tasks performed concurrent with perceptual tasks can interfere with each other. They suggest that when a pursuit task is performed simultaneously with a perceptual task, the accuracy of the psychophysical judgments may be impaired due to the attention directed toward the pursuit task. Murphy (1978) has also reported what may be interpreted as interference between oculomotor tasks and perceptual tasks. His subjects reported an inability to smoothly pursue a point moving over a stationary grating while simultaneously judging the contrast of the grating.

In our study, subjects were asked to discriminate the speeds of two gratings while simultaneously pursuing a superimposed drifting bar. If subjects chose to sacrifice speed discrimination performance to ensure pursuit accuracy, or vice versa, then we should expect a systematic trade-off in performance between the two tasks. In Fig. 9 we plot speed discrimination thresholds against pursuit accuracy, i.e., gain, to examine the relationship between the two. If speed discrimination performance was sacrificed for pursuit accuracy, then thresholds should increase with increasing pursuit gain; there should be a positive linear relationship between the two variables.

The best fit regression lines are shown as solid and dashed lines for grating speeds of 2.0 and 0.5 deg/sec, respectively. Not only are the fits not statistically significant at the 0.05 level, they have *negative* slopes. There is no apparent trade-off between speed discrimination performance and pursuit accuracy in this experiment.

The role of the extra-retinal motion signal

Perhaps the present results can be accounted for by some type of interaction between the retinal image motion signals and extra-retinal motion signals. The extra-retinal signal is thought to reflect the movement of the eye and may be a copy of the efferent signals sent to the oculomotor system or proprioceptive feedback from the eye muscles. Wertheim (1981) has proposed that the perception of motion is based on a comparison between the retinal signal and the extra-retinal signal. He has postulated that object motion is perceived only when the magnitude between the two signals exceeds a threshold.

The extra-retinal signal's role in motion perception has

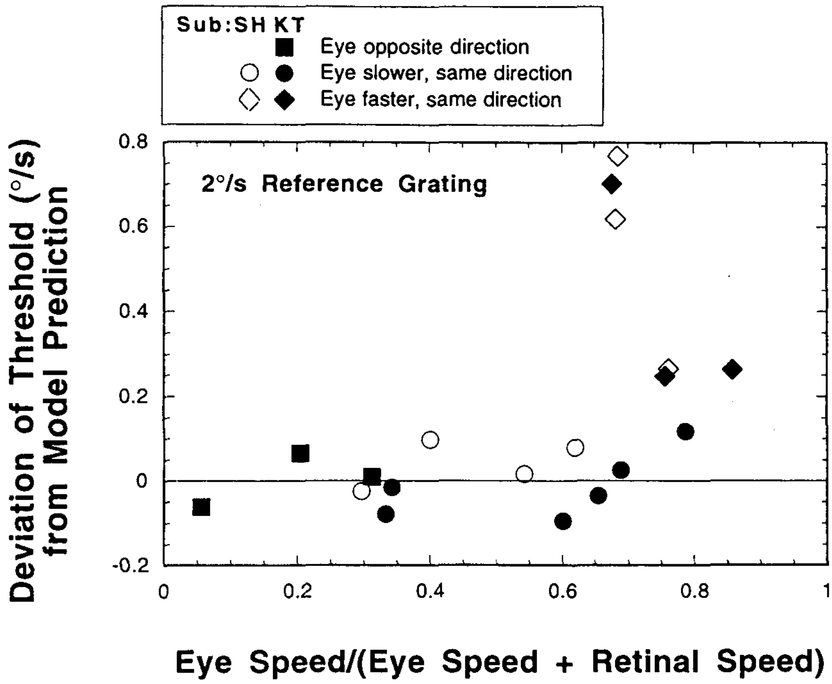


FIGURE 10. Magnitude of deviation of the speed discrimination thresholds from the model predictions plotted against the ratio of eye speed to the sum of eye speed and retinal speed. Solid symbols: subject KT; open symbols: subject SH. Squares: eye and grating moved in opposite directions; circles: eye and grating moved in the same direction, eye slower than grating; diamonds: eye and grating moved in the same direction, eye faster than grating. Grating speed = 2 deg/sec.

recently been investigated in a study by Brenner & van den Berg (1994). In their study, subjects judged eye velocity as they pursued a target moving against a textured background whose velocity was independently varied. Under certain conditions, pursuit target velocity was perceived to be constant regardless of changes in the velocity of the pursuit target or background, provided the relative motion between the two remained the same. In other conditions, perceived eye velocity was less than expected from the relative motion hypothesis They suggested that both retinal and extra-retinal signals contribute to an internal representation upon which velocities are judged. When the background moves at a slow speed in the same direction as the target or when the background moves in the opposite direction to the target, judgments are in agreement with the relative motion predictions. But when the background moves at a fast speed in the same direction as the pursuit target, subjects depart from motion relative to the background for their judgments of object velocity.

This asymmetry in results is similar to what we found in our experiment, but the direction of the asymmetry appears reversed in the two studies. In our study, performance deviated from a retinal motion hypothesis only when the *eye* moved at a fast velocity in the same direction as the grating. In the Brenner and van den Berg study, performance deviated from the relative motion hypothesis when the *background* moved at a fast velocity in the same direction as the pursuit target.

The apparent discrepancy can be resolved when one considers the differences between tasks for the two studies. In the Brenner and van den Berg study, subjects were instructed to judge the eye velocity, not the background velocity. In our study, the subjects were instructed to judge the grating velocity, not the eye velocity. It is likely that the strengths of the retinal and extra-retinal signals were differentially weighted in the two tasks. Interestingly, the results of *both* studies suggest an interaction between the two signals when the component not judged becomes large, relative to the sum of the two signals.

In Fig. 10, we have replotted the converted psychophysical thresholds of Fig. 6 (grating = 2.0 deg/sec). Assuming that the magnitude of the extra-retinal signal equals eye speed and the magnitude of the retinal signal equals retinal image speed, the abscissa in Fig. 10 is the proportion of the extra-retinal signal to the combined motion signals. The ordinate is the amount of deviation of the speed discrimination thresholds from the retinal motion prediction. The different symbols represent data of the three cases; data of Case 1 are shown as squares, data of Case 2 are shown as circles and data of Case 3 are shown as diamonds. Data that fall on the horizontal line at 0 are consistent with the retinal motion prediction.

Notice that the speed discrimination thresholds deviate from the retinal motion prediction when the relative magnitude of the extra-retinal signal is high. It is only when the ratio is high that the eye movement has a detrimental effect on discrimination performance.

An alternative explanation, suggested by a reviewer, that does not incorporate an extra-retinal signal is that the perceptual system may compare or pool two representations, one corresponding to retinal image motion and a second corresponding to distal stimulus motion (i.e., world frame motion). When the retinal image and distal stimulus motion are in the same direction, as in Cases 1 and 2, thresholds follow the prediction; however, when the retinal image and distal stimulus motion are in opposite directions, as in Case 3, thresholds do not follow the prediction. Although this parsimonious description can account for the data, tangentially related studies suggest that the perceptual system does not code velocity information in terms of a world frame (McKee & Welch, 1989).

In conclusion, eye movements can affect the ability to discriminate small differences in the speed of distal stimuli. Speed discrimination performance declines when the eye moves in a direction opposite the distal stimuli, as well as when the eye moves in the same direction but at a faster speed. For some conditions, the simulation predictions generated by a Monte Carlo method based on the retinal motion hypothesis provided a good match to psychophysical data. For conditions where the eye moved at a faster speed than the distal stimuli in the same direction, there was a large discrepancy between data and prediction. Under these conditions, it may be that the extra-retinal signal interferes with the retinal motion signals for speed judgments. Control experiments and analyses ruled out explanations for the discrepancy based on relative motion cues, attentional interference and saccadic involvement.

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